EOCENE AND OLIGOCENE FLORAS AND VEGETATION OF THE ROCKY MOUNTAINS[1]

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ABSTRACT

The Eocene and Oligocene epochs were times of major evolutionary, biogeographic, and vegetational changes in terrestrial plants. From a floristic perspective three major trends characterize this period in the Rocky Mountain region: 1) development of more distinct phytogeographic provinces from a relatively homogeneous Paleocene holarctic flora, 2) the early diversification in Eocene upland areas of presently important temperate families, and 3) the first appearances of many extant angiosperm genera and disappearance of many typically Cretaceous and Paleocene forms. From a vegetational perspective there are two strong trends. Initially there was an early Eocene spread of broad-leaved, evergreen forest to high northern latitudes (60°N), possibly the greatest geographic coverage such vegetation ever achieved. This was followed by the subsequent fragmentation of these forests to produce more open vegetation of lower stature in many areas. These floristic and vegetational trends were of great consequence for angiosperm evolution and biogeography. They were also significant in creating the ecological milieu for the evolution of early and mid Tertiary animals.

The Paleogene rocks and fossils of the Rocky Mountains and adjacent areas provide an exceptional window on the flora and vegetation of the time and place. Eocene and Oligocene rocks cover some 40% of the surface of the state of Wyoming (106,000 km²), and their total outcrop area in the Rocky Mountain region is in the range of 300,000² km (Fig. 1). Over much of this vast outcrop, weathering has exposed the strata, making them available for paleontological and geological study. Eocene–Oligocene deposits from a variety of fluvial, lacustrine, and volcanically influenced settings have produced tens of thousands of fossils collected at hundreds of localities. These Paleogene sequences have the potential to yield one of the most complete and geographically extensive records of evolutionary and ecological change in a terrestrial biota. A century or more of paleontological and geological research has only begun to explore this potential, in part because of the vast area and great thickness of the sedimentary sequences.

This paper is intended to serve three goals. First, to set out the basic data on the location, stratigraphic positions, and relative ages of the fossil floras. Second, to summarize published work on Eocene and Oligocene flora and vegetation of the region and discuss previous hypotheses in light of current data. Third, to suggest new directions for future research aimed at a regional understanding of Paleogene floras that takes full advantage of the potential of such a widespread and prolific fossil record.

GEOLOGIC SETTING

The Rocky Mountain region is geologically diverse, and its Cenozoic history has been reviewed in a number of recent volumes (e.g., Robinson, 1972; Curtis, 1975; Flores & Kaplan, 1985). Eocene and Oligocene plant fossils are best known from the large intermontane basin fill deposits of the eastern Rocky Mountain area and from the primarily volcanic deposits of western Montana, northwestern Wyoming, Idaho, Oregon, and Washington. The separate depositional histories of these two areas are important for interpreting historical change in their floras.

The intermontane basins of the eastern Rocky Mountain area (Fig. 1) began to develop in the Late Cretaceous as parts of a relatively continuous Rocky Mountain foreland region that intermittently was covered by a mid-continent seaway. Uplift of local, initially east–west trending, mountain ranges during the latest Cretaceous–Paleocene began to divide the foreland basin into structurally, topographically, and sedimentologically discrete units. Consequently, each of the present intermontane basins has a separate Cenozoic history, yet some general trends have affected most or all of the basins.

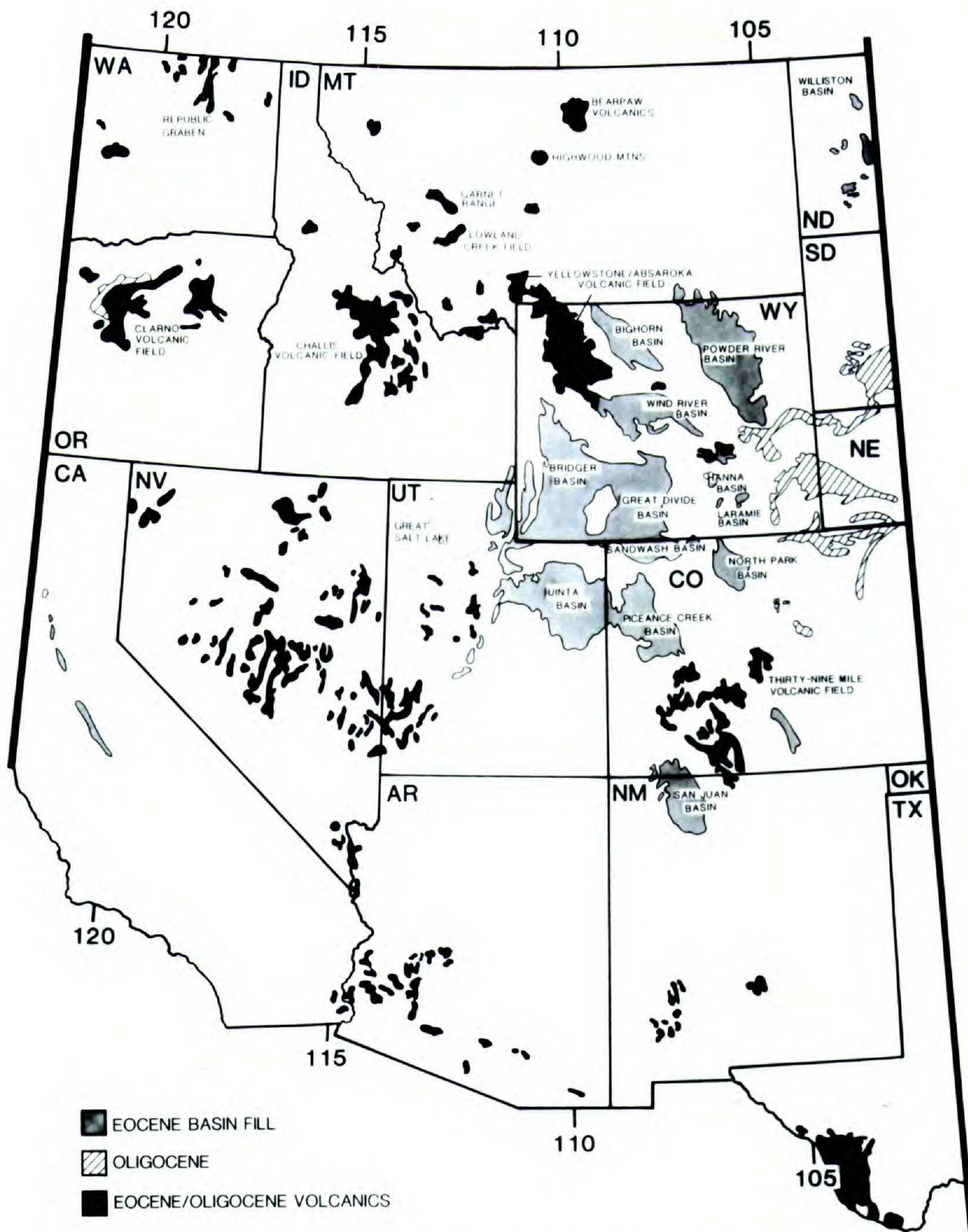Fluvial to paludal environments were preva-

FIGURE 1.   Outcrop area of Eocene and Oligocene rocks in the greater Rocky Mountain area.

lent throughout most of the area in the Paleocene and were environments of deposition for coals in the Powder River, Bighorn, Green River, and other basins. Fresh or brackish water lakes formed in the Uinta, Wind River, and Bighorn basins during the latter half of the Paleocene (Johnson, 1985; Keefer, 1965; Yuretich et al., 1984). Beginning in the Clarkforkian[3] and continuing into

the Wasatchian, paludal deposition of organic-rich sediment waned in most of the basins, and alluvial floodplain sediments began to be modified by oxidizing pedogenic processes (Bown, 1979; Bown & Kraus, 1981). The onset of this kind of pedogenic modification was probably controlled by a combination of local tectonic and physiographic factors, as well as by regional climatic change (Wing & Bown, 1985).

In the later Wasatchian and Bridgerian, large lakes again developed in many of the basins (Bighorn, Green River, Uinta–Piceance). In at least some cases this appears to reflect hydraulic closure of the basin rather than climatic change (Johnson, 1985), and the lakes of the Green River and Uinta–Piceance Basins are known to have been saline during much of their later histories.

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[3] Through much of this paper, North American provincial land mammal ages (NALMA) will be used in favor of standard epochal subdivisions because NALMA are known to be relatively synchronous throughout western North America (Flynn et al., 1984) and because it is easier to correlate floras with nearby mammalian sites than with the type age/stages of Europe. Correlation of NALMA with epochal boundaries and time are given in Figure 2.
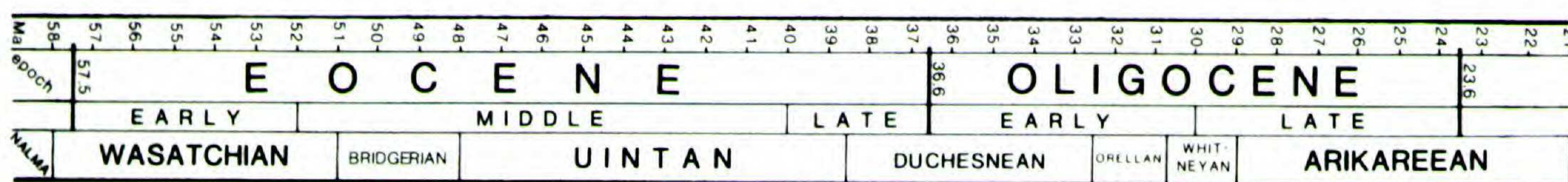
FIGURE 2. Correspondence of North American Land Mammal Ages (NALMA) with epochal and stage boundaries (after Berggren et al., 1985).

Much of the sediment filling these middle Eocene lakes and forming coeval fluvial deposits was derived from newly active volcanic fields in western Wyoming and Idaho.

During the later Bridgerian and Uintan most of the intermontane basins began to fill with sediment, and during the Duschesnean and Chadronian these sediments began to lap outward onto the tops of the bordering ranges. During the Oligocene, volcanically derived sediment continued accumulating at relatively slower rates in the eastern Rocky Mountains and Great Plains. Oligocene formations over much of the northern Rocky Mountains and Great Plains are typically thin, widespread units that were probably deposited on a surface of low relief.

The history of the volcanic centers in the western part of the northern Rocky Mountains is largely independent of that of the intermontane basin region. Volcanic activity was sporadic in southwestern Montana (the Elkhorn volcanic field) beginning in the latest Cretaceous and throughout the Paleocene (Roberts, 1972). However, the greatest pulse of volcanic activity began in the late Wasatchian to Bridgerian and continued through to the end of the Eocene.

From about 53 to 38 Ma there was volcanism across much of western Montana (Bearpaw, Garnet Range, Lowland Creek, Gallatin, and Beaverhead Canyon fields), northwestern Wyoming (Yellowstone–Absaroka Field), and Idaho (Challis Field), and in the Clarno area of Oregon, the Republic graben of northern Washington, and southern British Columbia (Chadwick, 1985). Although the intrusive and sedimentary rocks associated with these volcanic areas presently cover on the order of 10^5 km, it is likely that most of their original extent has been removed by erosion. Armstrong (1974) suggested that the Challis volcanic field once covered much of Idaho.

The extent and thickness of these broadly coeval volcanic deposits in the northern Rocky Mountain area indicate the region may have been a rugged, but more or less connected, volcanic highland during much of the Eocene (Axelrod,

1968; Fritz & Harrison, 1985). The prevalence of volcanic conglomerates and mudflows, and analogy with present day volcanic terrains, suggest strong topographic relief, which Fritz & Harrison (1985) estimated at 1,000–2,500 m difference between adjacent valleys and peaks.

Following the end of the Eocene, heavy volcanic activity shifted southward to southern Colorado, New Mexico, Arizona, and west Texas, and extensional tectonics began to affect the northern Rocky Mountains (Chadwick, 1985). A number of small, fault-bounded basins developed in western Montana during the Late Eocene and Oligocene. These basins filled with primarily fluvial and lacustrine deposits that were derived from both local sources and volcanics as far away as the Cascade Range of Oregon (Fields et al., 1985).

The geological events summarized above are highly relevant to the floristic and vegetational history of western North America. The development of a volcanic highland region in the northern Rocky Mountain region during the Eocene had several major effects on plant life, including: 1) dividing lowland areas that formerly had been continuous from the West Coast to the eastern Rocky Mountain region, 2) reducing the flow of Pacific-influenced air into the interior of North America, and 3) changing soil and groundwater conditions by the influx of airborne volcanic ash. Prior to and during the onset of these effects the low-lying area in the eastern Rocky Mountains was itself broken into a series of topographically isolated and somewhat climatically different basins. Thus the overall effect of geological events during the Eocene and Oligocene was fragmentation of a relatively homogeneous landscape along both north–south and east–west axes.

DISTRIBUTION OF FOSSIL FLORAS

No single source provides a comprehensive list of Tertiary plant localities in western North America. The list of localities given here (Appendix I) represents an attempt to bring together

the bulk of Eocene and Oligocene localities of the greater Rocky Mountain region. I estimate that this list is 60–80% complete.

The locality information was derived from a number of published and unpublished sources. Previous works listing a significant number of localities include those by Axelrod (1966a, 1966b, 1968), Axelrod & Raven (1985), Brown (1937), Hickey (1977), Leopold & MacGinitie (1972), MacGinitie (1941, 1953, 1969, 1974), and Wolfe (1981, 1985). Unpublished locality information was derived from collections at the U.S. National Museum of Natural History (including those of the USNM, the U.S. Geological Survey, and some formerly belonging to Princeton University), and from collections at the Museum of Paleontology (University of California, Berkeley) and the Yale Peabody Museum.

Not all of the 240 "localities" compiled here are strictly equivalent. Some floras commonly considered as units actually consist of the summed floral lists of a number of separate quarry sites (e.g., the Ruby paper shale flora of Becker, 1961, was collected at 15 quarries), whereas others were derived from a single excavation (e.g., Copper Basin flora of Axelrod, 1966a). Most of the listed localities are individual quarry sites, but for some floras listed in the literature it was not possible to determine how many sites contributed to the flora.

Criteria used in correlating and determining the ages of floral localities included mammalian biostratigraphy, lithostratigraphic equivalence, magnetic polarity stratigraphy, and radiometric dates. In order to avoid circularity, floras were *not* correlated on the basis of their taxonomic composition or physiognomic characteristics. The Tertiary time scale used here is that of Berggren et al. (1985). Chronological boundaries for North American Land Mammal Ages are from West et al. (in press), and Prothero (1985a, 1985b). There is controversy over the precise age of the Eocene/ Oligocene boundary. The date used here (36.6 Ma) is the most recent opinion, but many authors (e.g., Wolfe, this volume) use a date of about 34 Ma. Radiometric dates from older publications have been corrected for new constants using the tables published by Dalrymple (1979).

Fossil floras of Eocene and Oligocene age have a highly uneven geographic and stratigraphic distribution. Stratigraphically, the Wasatchian and Bridgerian are by far the best-represented time intervals, with the number of floras diminishing sharply through the Uintan and Duschesnean,

and into the Oligocene (Fig. 3). Geographically, the northern Rocky Mountain region is far better sampled than the southern region (Fig. 4). These inequities in distribution result from at least four factors. 1) Bias of the author: my work has centered on the lower Eocene of Wyoming, so I am particularly aware of these localities. 2) Wasatchian, Bridgerian, and early Uintan sections are thicker and more widely exposed than later Eocene and Oligocene rocks. 3) Later Eocene and Oligocene rocks are generally less fossiliferous than early Eocene rocks, probably reflecting less favorable conditions for plant preservation associated with a drying climate in the Western Interior. 4) Collecting has been more intense in some areas than in others.

In addition to the uneven distribution of floras in space and time, there are also changes through time in environments of deposition. Nearly all Wasatchian plant assemblages were recovered from rocks deposited in fluvial or fluvial/paludal settings. Although some Bridgerian and later floras are from fluvial deposits, the best known (e.g., Green River, Florissant) are from lacustrine sediments. Floral samples drawn from fluvial environments represent the flora differently than do those from lacustrine environments.

Fluvial assemblages, particularly those deposited on low-energy flood basins, are largely derived from local vegetation (Scheihing & Pfefferkorn, 1984; Spicer & Greer, 1986; Burnham, in press). This results in considerable spatial heterogeneity in the fossil assemblage that probably reflects original variation in the local vegetation (Hickey, 1980; Wing, 1980, 1984).

By contrast, lakes receive input from surrounding lakeshore vegetation and from inflowing rivers (Spicer, 1981). These different elements may be mixed to various degrees and scattered across the lake bottom. Although lacustrine assemblages are overwhelmingly dominated by plant parts derived from nearby vegetation (Drake & Burrows, 1980; Spicer & Wolfe, 1987), they tend not to preserve in situ variation in vegetation. They may, however, preserve more of the species that were present in the regional flora. As a result of being derived from a larger source area and of predepositional transport and mixing, lacustrine assemblages are probably more diverse than fluvial assemblages, and specimens are more evenly distributed among the taxa present.

As a consequence of the inequities in distribution of fossil floras and nonequivalence in their
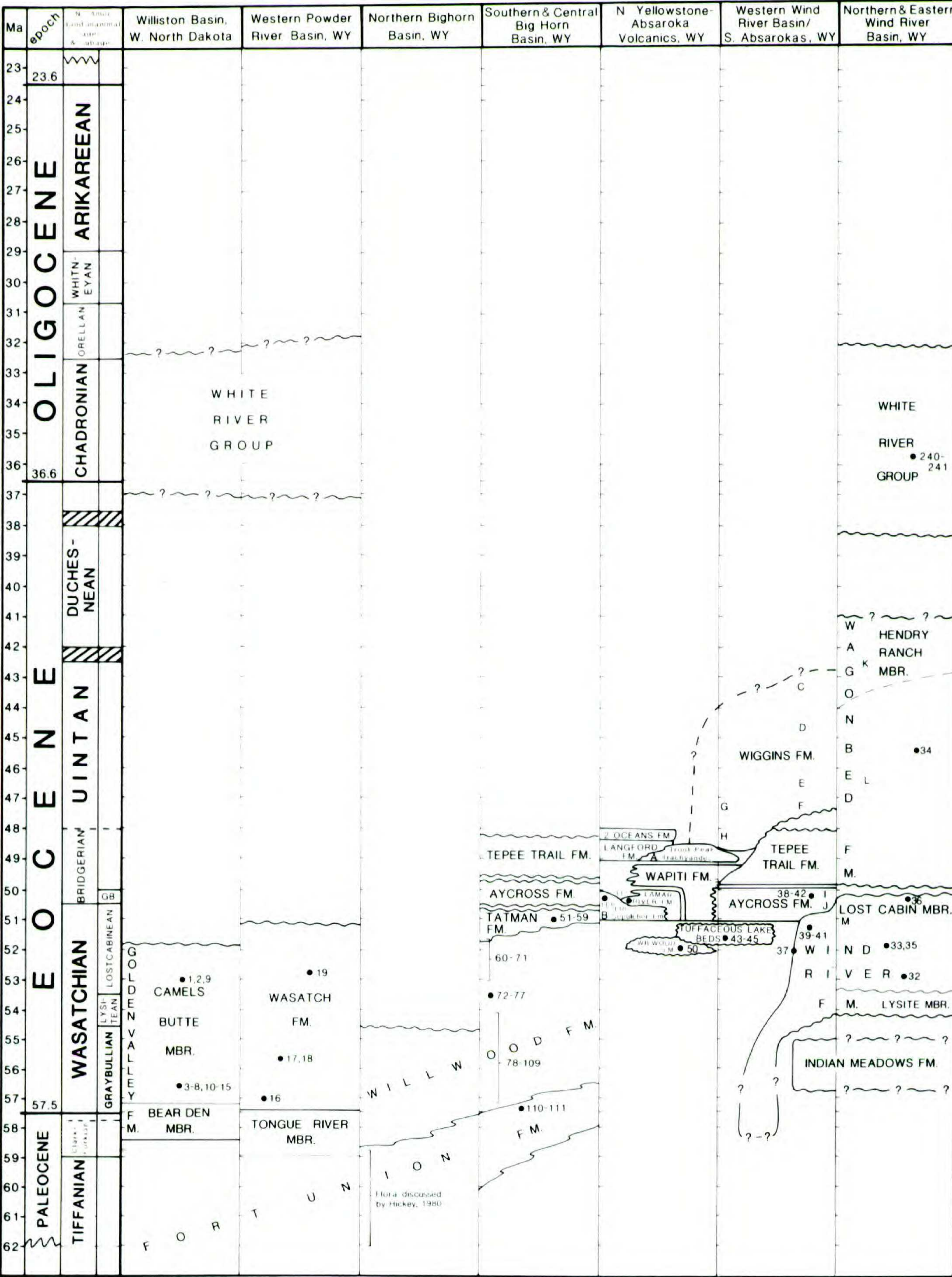
FIGURE 3. Correlation chart of Eocene and Oligocene floras from the Rocky Mountains and surrounding areas. Numbers indicate floras listed in Appendix I; letters (A–FF) indicate radiometric dates listed in Table 1.
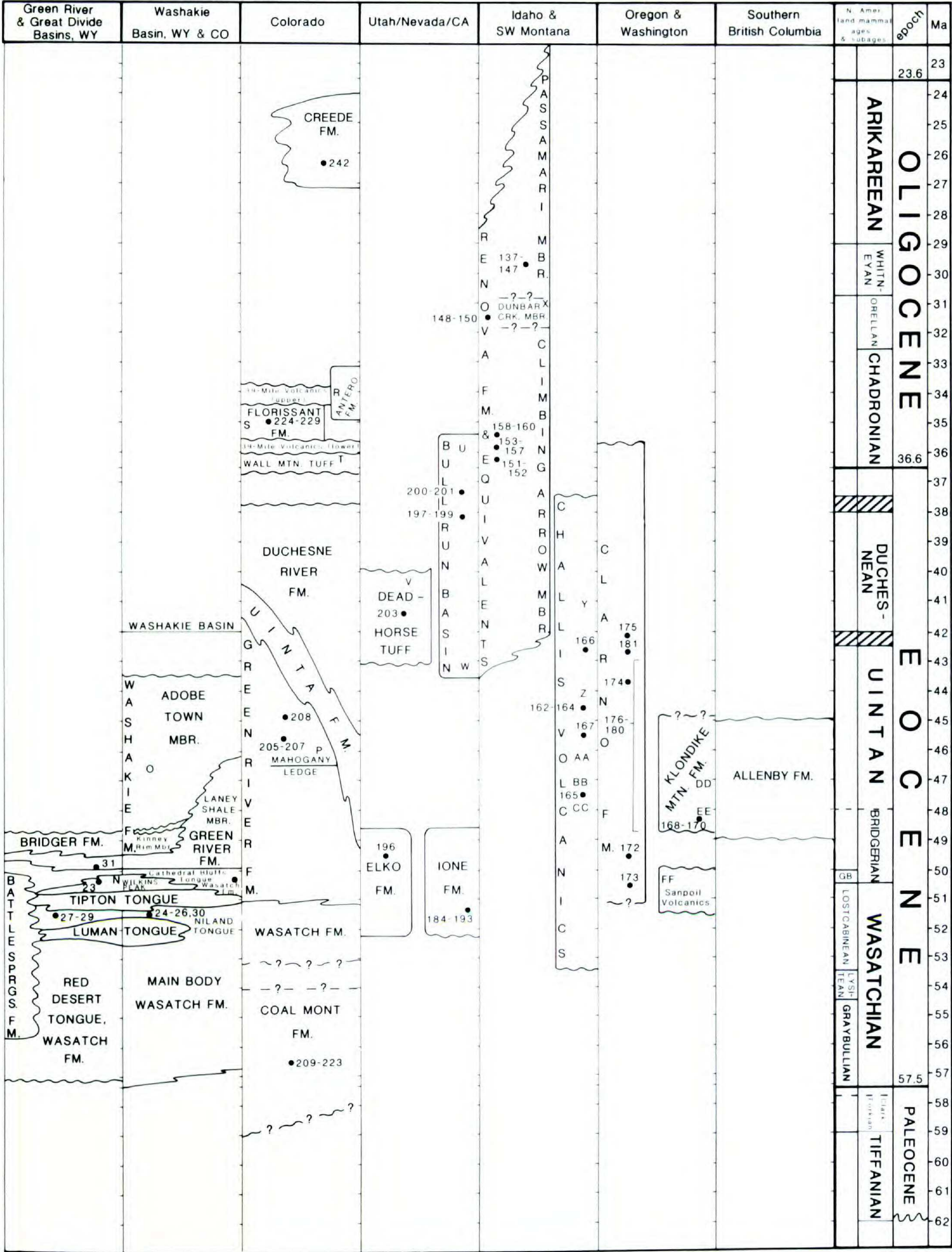
FIGURE 3.   Continued.

Table 1.   Radiometric dates of Tertiary floras in Figure 3.

Age	Stratigraphic Unit	Publication
A, 49.2 ± 0.7	Trout Peak Trachyandesite	Smedes & Prostka, 1972
B, 50.5 ± 1.55	Sepulcher Formation	Smedes & Prostka, 1972
C, 43.1	Wiggins Formation	Bown, 1982
D, 44.6	Wiggins Formation	Bown, 1982
E, 46.7	Wiggins Formation	Bown, 1982
F, 47.1	Wiggins Formation	Bown, 1982
G, 47.9 ± 0.5	Wiggins Formation	Bown, 1982
H, 48.5	Wiggins Formation	Bown, 1982
I, 50.4	Aycross Formation	MacGinitie, 1974
J, 50.6	Aycross Formation	MacGinitie, 1974
K, 42.3 ± 1.4	Henry Ranch Member, Wagon Bed Formation	Black, 1969
L, 46.2	Wagon Bed Formation, near Badwater, Wyoming	Evernden et al., 1964
M, 50.5	Halfway Draw Tuff, Wind River Formation	Evernden et al., 1964
N, 50.2	Little Mountain Tuff, Wilkins Peak Member, Green River Formation	Mauger, 1977
O, 46.7 ± 0.9	Washakie Formation, Bed 664 of Roehler	Mauger, 1977
P, 46.2	several hundred feet above Mahogany Ledge, Parachute Creek Member, Green River Formation	MacGinitie, 1974
Q, 26.5	Creede Formation	Axelrod, 1987
R, 34	Antero Formation	Epis & Chapin, 1975
S, 35	Florissant Formation	Epis & Chapin, 1975
T, 36–37	Wall Mountain Tuff	Epis & Chapin, 1975
U, 36	"Chicken Creek Formation," 5 feet above highest floral locality	Axelrod, 1966b
V, 41 ± 1	Deadhorse Tuff	Axelrod, 1966b
W, 43	"Frost Creek Formation," 1,500 feet below lowest floral locality	Axelrod, 1966b
X, 31.1	Williams Creek basalt	Fields et al., 1985
Y, 41.1 ± 1.6	Salmon area tuffs	Fritz & Harrison, 1985
Z, 44.2 ± 1.7	Salmon area tuffs	Fritz & Harrison, 1985
AA, 46.3 ± 1.0	rhyolite below "Dewey Beds"	Fritz & Harrison, 1985
BB, 47.2 ± 1.8	basalt above Germer Tuffaceous member	Edelman, 1975
CC, 48.0 ± 1.0	Latite-andesite Member, Challis Volcanics	Edelman, 1975
DD, 47.0 ± 1.8	Klondike Mountain Formation	Wolfe & Wehr, 1987
EE, 48.2 ± 1.6	Klondike Mountain Formation	Wolfe & Wehr, 1987
FF, 50–51	Sanpoil Volcanics	Wolfe & Wehr, 1987

depositional environments, there are obvious difficulties in interpreting patterns of vegetational and floristic change through time. In spite of these difficulties, a number of durable generalizations have emerged concerning the early Tertiary development of the Rocky Mountain flora.

Floristic and Vegetational History

Three major floristic trends are indicated by Eocene–Oligocene fossil assemblages from the Rocky Mountain area: the modernization of the angiosperm flora at the generic level, the breakup of the Paleocene North American province into distinct phytogeographic subregions, and the major diversification of many present-day mi-crothermal lineages (e.g., Rosaceae, Betulaceae, Aceraceae). There were also three major vegetational periods during the Eocene and Oligocene. During the Wasatchian and Bridgerian there appears to have been a major poleward expansion of subtropical and paratropical forest types in response to global climatic warming (Wolfe, 1985). Perhaps beginning as early as the Clarkforkian in some areas, and of increasing importance during Bridgerian and later time, there is evidence that these forests were replaced in some parts of the region by more open subtropical vegetation of lower stature, probably as a result of local or regional orographic drying (e.g., MacGinitie, 1969). Finally, during the latest
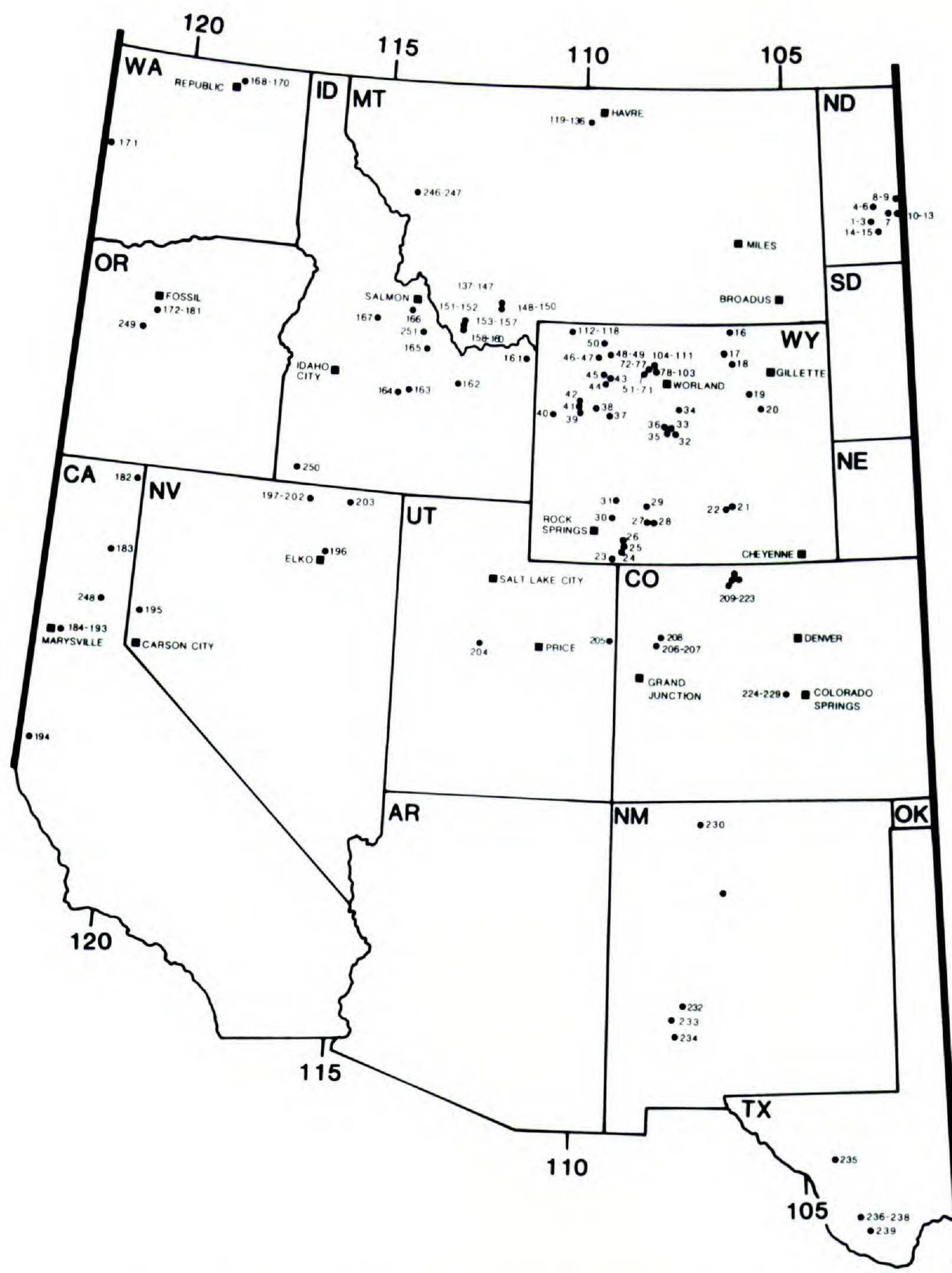
FIGURE 4. Map position of Eocene and Oligocene floras mentioned in the text and in Figure 3. Numbers refer to floras listed in Appendix I.

Eocene and Oligocene, vegetation of the Rocky Mountain region became dominated by a mixture of conifers and broad-leaved deciduous forms.

MODERNIZATION

Paleobotanical systematics of the last century and early in this century was based largely on superficial characteristics of leaves. This led to exaggerated estimates of the similiarities between extinct and modern floras. More recent systematic work has focused on detailed comparisons of leaf venation (e.g., Hickey, 1977) and on greater use of multiple organs (e.g., Manchester, 1986). One result of such work has been

the realization that many Paleocene angiosperms represent extinct genera or intermediates between several related living genera.

In contrast, many, if not most, angiosperm remains younger than Late Eocene can be assigned to extant genera with little ambiguity, although sectional or other subgeneric-level affinities may be unclear (see Manchester & Crane, 1983 and Wolfe & Tanai, 1987 for well-documented exceptions). The temporal pattern of appearance of extant genera has not been quantified, nor has it been determined the extent to which this modernization reflects evolution within lineages as opposed to extinction of archaic lines and replacement by modern ones. Al-

though this generic modernization of angiosperms is a striking systematic pattern, little has been said about its biological significance. Modernization at the generic level may reflect a true radiation of angiosperms, perhaps in response to changing climatic and topographic conditions in western North America, or it may be an artifact of our retrospective view. That is, the appearance of many modern genera in the Eocene occurred because angiosperms in a number of independent lineages accumulated enough recognizable generic characters to be pigeonholed easily in present-day categories. This question could be resolved by measuring and comparing rates of morphological change during the Paleocene and Eocene.

PROVINCIALITY

The Eocene divergence of Rocky Mountain and West Coast floras and its relationship to East Asian–North American disjunct distributions in a number of living plant groups is probably the most discussed aspect of the Tertiary paleobotanical record in western North America (e.g., MacGinitie, 1941; Leopold & MacGinitie, 1972; Wolfe, 1972; Hickey, 1977). Consequently, I will summarize the pattern only briefly.

Paleocene floras from across northern North America and to some extent of Europe and Siberia are relatively homogeneous (Wolfe, 1966). Leaf assemblages typically are of low diversity and dominated by a group of taxa including *Ginkgo, Metasequoia, Glyptostrobus, Macginitiea* ("*Platanus*") *nobilis*, "*Carya*" *antiquorum*, "*Ampelopsis*" *acerifolia*, and members of the *Cercidiphyllum* complex, among others. Such floras have been reported from Alaska (Wolfe, 1972), many areas of the northern conterminous U.S. (Brown, 1962), the Canadian high Arctic (Hickey et al., 1983), and Greenland (Koch, 1963).

Because some of these Holarctic Paleocene taxa (e.g., *Metasequoia, Cercidiphyllum*) are now East Asian endemics, Paleocene floras sometimes have been described as having "East Asian" affinities (although they are only East Asian in a modern context). During the Eocene many of these Paleocene ("East Asian") forms were eliminated from floras in the eastern Rocky Mountains, presumably as a result of their inability to withstand seasonal dryness (Leopold & MacGinitie, 1972). In contrast, some of the same lineages survived into the Neogene along the West Coast and in

the northern intermountain region of North America. At the same time that the "East Asian" forms were being eliminated in the eastern Rocky Mountains, some of the new genera appearing there were "Central American"; that is, their closest living relatives are in the seasonally dry subtropics of Mexico and Central America (MacGinitie, 1969; Leopold & MacGinitie, 1972). This general pattern has been confirmed by additional work in the intermontane basins of the eastern Rocky Mountains, but three modifications should be noted.

Paleocene megafloral samples may be more uniform than actual Paleocene floras because the fossil assemblages have been collected from a limited and similar array of paleoenvironments that tend to have low floral diversity. This would accentuate the impression that a homogeneous floral province was being broken up in the Eocene.

The regional extinction of taxa with East Asian affinities and the appearance of taxa with Central American affinities began in the Clarkforkian and was well under way in some areas by the mid Wasatchian, considerably earlier than was recognized by Leopold & MacGinitie (1972), who lacked floras from the Paleocene–Eocene transition period. Clarkforkian taxa with closest living relatives in Central America include *Chaetoptelea microphylla, Woodwardia gravida*, and species of *Populus* sect. *Abaso*. By late Graybullian or Lysitean time, some taxa with closest living relatives in East Asia, such as *Metasequoia* and some members of the *Cercidiphyllum* complex, were already regionally extinct in basinal floras of the eastern Rocky Mountains.

The shift from East Asian to Central American affinities in the flora of the eastern Rocky Mountains was not a uniform process, and some significant taxa do not follow the pattern. For instance, the genus *Platycarya*, now confined to East Asia, did not appear in western North America until the early Wasatchian and achieved maximum abundance throughout the region in the latest Wasatchian and early Bridgerian before going regionally extinct (Leopold & MacGinitie, 1972; Wing & Hickey, 1984). This pattern also appears to hold true for several undescribed species in the Icacinaceae, Flacourtiaceae, and Menispermaceae. *Ailanthus*, also now endemic to East Asia, appeared in North America during the early to mid Eocene (Chalk Bluffs flora, Green River flora, Rate Homestead flora, MacGinitie, 1941, 1969), and was abundant in Oligocene floras from southwestern Montana (Becker, 1961,

1969) before going regionally extinct in the later Tertiary.

Floristic segregation of northern and southern areas was probably occurring at the same time as the better-documented and better-discussed east–west divergence (Axelrod & Raven, 1985). Unfortunately, few Wasatchian–Bridgerian floras have been reported from the southern Rocky Mountains (Fig. 4). One small Lysitean flora from the San Juan Basin (Tidwell et al., 1981) shows that two taxa common in the Gardnerbuttean and Bridgerian of Wyoming ("*Sapindus*" *dentonii* and *Eugenia americana*) appeared two to three million years earlier in New Mexico. This suggests the possibility that some taxa were migrating northward during the climatic warming of the early Eocene. A similar geographic pattern has been observed in some mammalian species (Beard, pers. comm., 1986).

DIVERSIFICATION OF MICROTHERMAL LINEAGES

The Wasatchian and Bridgerian floras from the eastern Rocky Mountain region are a mixture of taxa now associated with temperate and subtropical to paratropical climates. For instance, mesothermal to microthermal groups like the Betulaceae (*Alnus, Paleocarpinus*), Cercidiphyllaceae, and Hamamelidaceae (Hamamelidoideae) are frequently associated with members of megathermal groups such as the Icacinaceae (*Paleophytocrene*), Lauraceae (*Phoebe*), Palmae, and Cyatheaceae (*Cnemidaria*). In most of these floras the microthermal elements are not diverse, although they may be important in terms of abundance (Wolfe, 1972, 1977).

In contrast, floras of similar or somewhat younger age from the volcanic areas farther west may be strongly dominated in both abundance and diversity by microthermal taxa. This has been attributed to the relatively high paleoelevation of these floras (Axelrod, 1966b, 1968; Wolfe & Wehr, 1987). Currently the best known of these floras is from Republic, Washington (Fig. 4; Wolfe & Wehr, 1987, and unpubl.). The vegetation at Republic is inferred to have been a Mixed Coniferous forest, but the diversity of microthermal angiosperm groups is striking: Hamamelidoideae, 4 species; Fagaceae, 4 species; Betulaceae, 5 species; Rosaceae, 19 species; Aceraceae, 7 species (Wolfe & Wehr, 1987; pers. comm., 1987). Although the Copper Basin flora of northern Nevada (Axelrod, 1966a) is younger and less diverse, it shows a similar domination by mi-

crothermal taxa. *Alnus* is represented by 2 species, one of which accounts for 85% of the specimens, and there are 3 species of *Mahonia*, 6 of Rosaceae, 3 of *Acer*, and 3 of Ericaceae.

Although upland floras of Paleocene or greater age are not known, it seems possible that the first major diversification of many present-day microthermal lineages took place during the Eocene in upland areas like the volcanic highland of the northwestern United States (Wolfe, 1986, this volume). Some of these groups were represented by relatively generalized species in later Paleocene or early Eocene lowland floras. Thus the adjustment of basically megathermal or mesothermal lines to cooler climates initially may have taken place along altitudinal gradients (Wolfe, pers. comm., 1986). Following mid-Tertiary climatic cooling, these upland lineages spread and diversified over much of the Northern Hemisphere, whereas their megathermal or mesothermal sister taxa now have relictual southerly distributions.

One particularly good example of this pattern is seen in the genus *Populus*. Species of the primitive section *Abaso* are common in Clarkforkian, Wasatchian, and Bridgerian floras over much of North America (Eckenwalder, 1977; Wing, 1981), usually in lowland settings, although *Populus adamantea* does occur in probable Oligocene upland floras described by Becker (1960, 1972, 1973). The extant species of this section, *P. mexicana*, is distributed only in limited parts of northeastern and northwestern Mexico. The earliest record of the more advanced sections that account for most of the present-day diversity and distribution of the genus is in the late Eocene Bull Run flora (Axelrod, 1966a). A number of species belonging to the more advanced sections are common in later Tertiary floras, but there is no known fossil record of sect. *Abaso* poplars following the early Oligocene.

PATTERNS OF VEGETATIONAL CHANGE

The general pattern of vegetational change during the Eocene and Oligocene in western North America has been outlined in a number of publications (e.g., Axelrod, 1958, 1968; Axelrod & Raven, 1985; MacGinitie, 1941, 1969; Wolfe, 1971, 1975, 1985). Despite considerable disagreement on details, there is overall agreement about the large-scale trends. Broad-leaved evergreen forests were dominant over most of the area during most of the Eocene, with two main

exceptions. Some areas in the eastern Rocky Mountains may have been dry enough to create more open, partially deciduous vegetation. Volcanic activity in the western Rockies during the late Wasatchian, Bridgerian, and Uintan generated uplands where conifers and broad-leaved deciduous taxa became important components of the vegetation. Climatic cooling and drying during the late Eocene and Oligocene brought about increasing dominance of mixed coniferous and broad-leaved deciduous forest.

Late Paleocene vegetation in most areas of western North America was broad-leaved evergreen forest with an admixture of deciduous elements (e.g., Golden Valley flora of Hickey, 1977). During the latest Paleocene and early Eocene (Wasatchian) world climates were warming (Savin, 1977; Wolfe, 1971, 1978; Wolfe & Poore, 1982), possibly as a result of elevated levels of atmospheric CO_2 and associated effects on circulation patterns (Owen & Rea, 1985; Rea et al., 1985). At this time evergreen broad-leaved taxa increased in importance within local floras.

Floras from the Willwood Formation of northwestern Wyoming span most of the Wasatchian and show an upward increase in the number of entire-margined (41% to 52%) and thick-textured leaves, although there are also changes in sedimentary environment that may be causally related to this shift (Wing, 1981). Using data on living vegetation presented by Wolfe (1979), these leaf-margin percentages correspond with Microphyllous or Notophyllous Broad-leaved Evergreen Forest. Wolfe (1985) interpreted slightly older (Clarkforkian) floras from the adjacent Powder River Basin as representing Paratropical Rainforest, suggesting that an overrepresentation of streamside taxa in Bighorn Basin floras from the Fort Union and Willwood formations, or a relatively higher elevation, has given them a "cooler" aspect. I think it more likely that the less entire-margined, presumably more deciduous, floras of the Bighorn Basin were under the influence of a seasonally dry climate as early as the middle Clarkforkian. This is also suggested by the development of oxidized soil horizons in floodplain sediments of this age in the Bighorn Basin (Gingerich et al., 1980). A resolution of this apparent conflict would involve detailed comparison of depositional settings of the floras or independent evidence for paleoelevation. Regardless of these somewhat different interpretations of vegetation in northern Wyoming, it is apparent that some form of broad-leaved ever-

green forest extended as far north as 65° during the Wasatchian (Wolfe, 1985).

A great many Lostcabinian-aged (late Wasatchian) fossil localities are known from all over the state of Wyoming and from the Golden Valley Formation of western North Dakota (e.g., numbers 1, 2, 9, 19, 27–30, 32–33, 50–71; Fig. 3, Appendix I). These floras are mostly uniform in composition and dominated by one of two species of *Platycarya*, with important subdominants being *Alnus*, "*Dombeya*" *novi-mundi*, "*Dalbergia*," *Zingiberopsis isonervosa*, and species of Icacinaceae, Lauraceae, Magnoliales, and Palmae. Common pteridophytes are *Cnemidaria magna*, *Lygodium kaulfussii*, *Thelypteris weedii*, *T. iddingsii*, and a large-statured species of *Equisetum*. The similarity in these floras may in part reflect similar environments of deposition occurring in a number of intermontane basins at approximately the same time. Given, however, that some range of depositional environments is spanned by these floras, it is likely that the successional vegetation most likely to be preserved in fluvial sediments was truly similar over this large region. This in turn implies the existence of few sharp climatic differences across the area, which is in distinct contrast with the early Bridgerian floras discussed in the next section.

Vegetation during early Bridgerian time (about 50 Ma). Although the latest Wasatchian and Bridgerian were the times of maximum poleward extent of broad-leaved evergreen forests, vegetation of the Rocky Mountain region began to differentiate more strongly during this time interval. This differentiation is illustrated by comparing four floras: the Little Mountain flora from the upper Wilkins Peak Member of the Green River Formation in southern Wyoming (23 in Figs. 3 & 4, Appendix I), the Boysen flora from the upper part of the Wind River Formation in the northcentral Wind River Basin (36), the Kisinger Lakes-Tipperary flora from the Aycross Formation in the western Wind River Basin (38, 42), and the flora of the lower Sepulcher and Lamar River formations in Yellowstone National Park in northwestern Wyoming (112–118). All four of these floras are approximately 50–51 Ma and correlate with Gardnerbuttean (early Bridgerian) mammalian faunas.

Based on floristic affinities, foliar physiognomy, and sedimentological data, MacGinitie (1969) inferred that the Little Mountain flora was

derived from open woodland vegetation. (MacGinitie used the term "savanna woodland," although he pointed out this might misleadingly imply that grasses played an important role in the vegetation.) More recently, Wolfe (1985) stated that leaf size in the Green River floras is too large for scrub or savanna vegetation and is more consistent with semideciduous subtropical to paratropical forest. The 22 species of dicotyledonous leaves from the Little Mountain flora are generally small and thick textured, and a number of the species belong to families or genera typical of seasonally dry subtropical vegetation (e.g., *Alchornea, Cardiospermum, Populus* sect. *Abaso,* and a number of microphyllous Leguminosae; MacGinitie, 1969: 67–68). Recent sedimentological work on the Wilkins Peak Member suggests that deposition took place in and around the margins of a playa lake that lay in an orographic desert basin (Smoot, 1983). The upper part of the Wilkins Peak Member apparently represents the maximum transgression of the lake and hence the wettest period during the deposition of this part of the Green River Formation (Smoot, 1983).

The Boysen flora is largely undescribed, although it was referred to in a treatment of the Green River flora (MacGinitie, 1969). This flora occurs in fluvially deposited, irregularly fissile, tuffaceous mudstones at the southern edge of the Owl Creek Mountains. The assemblage has approximately 15 species and is heavily dominated by palm leaves, *Lygodium kaulfussii,* and an entire-margined dicot leaf resembling *Sapindus* spp. Other common elements include "*Populus*" *wyomingiana, Canavalia diuturna,* cf. *Typha, Zingiberopsis isonervosa,* and *Musophyllum complicatum.* The importance of palms, herbaceous monocots, and vines suggests low-stature, perhaps relatively open, floodplain vegetation. Somewhat similar vegetation may have been responsible for forming the Lostcabinian-aged Vermillion Creek coal in southern Wyoming (Nichols, in press).

The Kissinger Lakes-Tipperary flora consists of 5 ferns, 1 horsetail, 2 conifers (*Glyptostrobus* and *Chamaecyparis*), and 44 angiosperms (MacGinitie, 1974). Of the 36 well-defined dicotyledonous leaf types, 55% have nonentire margins, and judging by their closest living relatives, some 60% were deciduous. A number of the genera in the fossil assemblage are presently restricted to subtropical or tropical climates (e.g., *Acrostichum, Apeiba, Canavalia, Dendropanax,*

Thelypteris). Based on foliar physiognomy and the distribution of living relatives, MacGinitie (1974) inferred that the Kisinger Lakes flora was derived from a subtropical to tropical, semideciduous forest resembling those native to the southwest coast of Mexico at elevations of about 1,000 m. These inferences are consistent with the diverse palynoflora, which in most samples is dominated by angiosperms and ferns (Leopold, 1974).

The fossil floras of Yellowstone National Park were first described by Knowlton (1899) and have not been subjected to a general revision since. Therefore, most of the published identifications are probably incorrect. Furthermore, much of the megafossil material comes from sites that are imprecisely located and of unknown stratigraphic relationship. It may be that significant temporal change within the "Yellowstone flora" has remained undetected as a result. In spite of these problems, most of the Yellowstone assemblages were derived from vegetation that was quite different from the kind inferred for the assemblages discussed above.

Four genera of conifers are known from megafossil remains (*Sequoia, Glyptostrobus, Pinus,* and ?*Podocarpus*), and the first three are abundant at many localities (Dorf, 1960; Aguirre, 1977). As might be expected, the importance of conifers is even more strongly indicated by the palynoflora, where they are diverse (12 genera) and consistently make up about half of the flora (Fisk, 1976). Ferns are also highly diverse and abundant at many localities in the Sepulcher Formation. Fisk (1976) reported 28 species of pteridophyte spores from the Yellowstone Park palynoflora, and there are 10–15 named species from the macroflora. The local abundance of ferns at some localities (particularly *Thelypteris weedii* and *Allantoidiopsis erosa*) may be related to the frequency of disturbance by volcanic events. A similar dominance of ferns in the colonizing vegetation has been noted following eruption and deposition in the vicinity of El Chichón volcano in Mexico (Spicer et al., 1985).

The foliar physiognomy of the Yellowstone National Park floras has not been studied in detail, but dicot leaves in the collections at the U.S. National Museum of Natural History are mostly in the notophyll and mesophyll size categories. Drip tips are present on a few taxa, and roughly half of the species have entire-margined leaves. Although the percentage of entire-margined species is similar at Yellowstone (approximately

50%) and Kisinger Lakes (54%), leaf size in the Kisinger Lakes flora is generally in the microphyll to notophyll range (Wing, unpubl. data; Wolfe, pers. comm., 1987). These physiognomic aspects of the Yellowstone assemblages, in addition to the importance of conifers, suggest that the vegetation grew under a somewhat cooler and perhaps less seasonally dry climate. The forest from which the Yellowstone flora was derived appears to have been a variety of broad-leaved evergreen forest that included a substantial element of conifers in some local environments.

The question of taphonomic mixing of floral assemblages is ever present but has been a particular focus of debate with regard to fossil floras from Yellowstone National Park (Fisk, 1976; Fritz & Fisk, 1978; Fritz, 1980a, 1980b, 1981a, 1981b; Retallack, 1981; Yuretich, 1984; Karowe & Jefferson, 1987). The mixture of "tropical" and "temperate" elements (e.g., *Thuja* and presumed evergreen members of the Lauraceae) in the Yellowstone floras has been attributed to transport of plant remains derived from vegetation growing at a range of elevations (Fisk, 1976; Fritz, 1980a, 1986), and the upright stumps and autochthonous "fossil forests" described by Knowlton (1899) and Dorf (1964) have been explained in part as the consequence of transport by mudflows associated with volcanic activity (Coffin, 1976; Fritz, 1980a, 1980b, 1986; Fritz & Harrison, 1985).

Observations of present-day volcanic systems have shown that high-energy mudflows can transport upright stumps from higher to lower elevations, and that stumps weighted by soil trapped in their roots may float upright for a time in lacustrine situations (Fritz, 1980a, 1980b, 1986; Coffin, 1983). Furthermore, sedimentological and stratigraphic studies of the Sepulcher and Lamar River formations and other Eocene volcanic units have highlighted the importance of high-energy deposits that are presumably indicators of steep paleotopography (Fritz, 1980c; Fritz & Harrison, 1985). In spite of these important observations, several lines of evidence suggest that the Yellowstone megafossil assemblages are not highly allochthonous.

First, although many fossil trees in the Specimen Ridge section may be prone rather than upright, this is not always the case. The presence of paleosols around some of the upright stumps is evidence that these were fossilized in place rather than transported upright to the site of burial and preservation (Retallack, 1981). Yuretich

(1984) and Karowe & Jefferson (1987) have presented petrographic and sedimentological evidence that the upright stumps are generally in situ. 1) Tree stumps are rooted in fine-grained sediments, not in conglomerates. 2) Some conglomerates have structures showing that they flowed around trunks in place. 3) Upper parts of inclined axes are abraded, but parts contained in finer-grained rock are not. 4) Petrographic sections of sediment containing fossil tree roots show no signs of extensive current bedding but do show indications of pedogenesis. Many of the leaf compression assemblages, which also show mixed "temperate" and "tropical" forms, are derived from fine-grained fluvial sediments and thus are unlikely to be highly transported (Wing, unpubl. data). Some fine- to medium-grained, airfall tuffs have the potential to entomb plant assemblages that quite accurately reflect local vegetation (Burnham & Spicer, 1986).

Second, the presence in the same sedimentary units of trees showing distinct seasonal growth with trees lacking distinct growth rings (Wheeler et al., 1977, 1978) has been cited as evidence that plants that grew under more than one climatic regime are present (Fritz & Fisk, 1978). This interpretation is not justified. Tree species have varying genetic capacities for seasonal growth, and individual trees are variably influenced by microclimatic and edaphic factors. The result is that different trees in the same region may show different patterns of growth (e.g., Tomlinson & Craighead, 1972). Fossil log assemblages containing specimens with both seasonal and aseasonal growth have been observed in sedimentary environments that could not have produced long-distance transport (Bown et al., 1982).

Third, most of the extreme examples of dissonance in the climatic tolerances of elements in the flora are generated by comparing the palynoflora with the megaflora. Pollen of *Abies* and *Larix* were less than 1% of the assemblages in which they occurred, which in turn were only a few of the 20 samples taken by Fisk (1976). Obviously, these could be highly allochthonous pollen grains derived from vegetation growing at higher elevations than the site of deposition. *Picea* occurred as 1–3 grains in 12 of the 20 samples, and reached 2%–6% of the flora in three samples (Fisk, 1976). Cross & Taggart (1982) have noted that abundance of *Picea* pollen is generally in rough proportion to its importance in the source vegetation, implying that spruce could have been

a minor part of local vegetation, probably at higher elevations in the watershed containing the site of deposition.

Fourth, almost all early Eocene floras from western North America contain some taxa that presently have mutually exclusive climatic requirements (MacGinitie, 1969, 1974; Wolfe, 1980). In many floras the depositional setting argues strongly against explaining the presence of these dissonant elements by transport. For instance, backswamp compression fossil assemblages from the Willwood Formation, perhaps one million years older than the Yellowstone flora, have abundant palms, *Cnemidaria* (cyatheaceous tree fern), and *Alnus* (Wing, 1981). The Willwood Formation is a mostly fine-grained, basin-fill formation deposited by low-energy streams (Bown, 1979); low paleotopography is further indicated by thin, laterally extensive sheet sands (Kraus, 1980) and paleosol horizons that are traceable over many kilometers (Bown & Kraus, 1981). Many of the collecting sites for the Willwood flora were near the center of the basin, at least 100 km from the uplifted basin margins. The assemblages were derived from fine-grained mudstones (Wing, 1984), and similar assemblages are characteristic of this lithology over a large part of Wyoming (Wing, unpubl. data). Given this depositional environment, the potential for long-distance transport of leaves is miniscule, and the assemblages must be autochthonous or transported only a short distance. Therefore there has been change through time in the climatic requirements of the taxa involved and/or early Tertiary climates permitted the coexistence of genera that at present have largely nonoverlapping ranges.

In conclusion, recent stratigraphic and sedimentological studies of volcanic strata in Yellowstone National Park and other Paleogene volcanic sequences have demonstrated the importance of high-energy mudflow deposition and have made it clear that such deposits are characterized by a high degree of lateral variability. However, these studies have failed to demonstrate that the majority of the megafossil assemblages from such deposits are allochthonous. Currently, prevailing evidence suggests that plant megafossils, especially compression assemblages of leaves, generally accumulated from local sources during quiet periods between violent, localized, mudflow deposition.

Although the Republic flora (168–170; Figs. 3, 4) is approximately 2 Ma younger than the four floras discussed above, it is similar to the Yellowstone flora in having abundant conifers in both the megaflora and palynoflora. Wolfe & Wehr (1987) argued that the Republic paleovegetation was a mixed coniferous forest dominated by conifers because: 1) *Chamaecyparis* and *Pinus* are abundant at the Graphite Creek locality, 2) bisaccate pollen dominates the palynoflora, and 3) conifers are quite diverse (including *Thuja, Abies, Picea, Tsuga,* and *Pseudolarix* in the megaflora). Deciduous angiosperms are the most abundant and diverse group at the other two localities, but broad-leaved evergreens are present, including *Phoebe, Photinia, Ternstroemites* spp., and a new extinct genus. Based on the physiognomy of the assemblage, Wolfe & Wehr (1987) inferred a mean annual temperature of 12–13°C and a mean annual range of temperature of 5–6°C. By comparing these temperature estimates with those inferred for approximately coeval floras from the Puget Group, Wolfe & Wehr (1987) estimated the paleoelevation of the Republic flora as 725–910 m. The greater importance of conifers and deciduous broad-leaved plants at Republic than in the Yellowstone flora probably does not reflect a higher paleoelevation if estimates for the two areas are even approximately correct. Therefore, the compositional and physiognomic differences between the two floras probably result from differing taphonomic processes, climatic cooling during Bridgerian time, or both.

Vegetation during the Chadronian (38–33 Ma). Comparison of the approximately contemporaneous Little Mountain, Boysen, Kisinger Lakes, and Yellowstone floras illustrates the kinds of vegetational and floristic differences that existed over one part of the northern Rockies at about 50 Ma. The regional importance of coniferous and broad-leaved deciduous elements seems to have increased during the later Eocene and Oligocene, with dominantly coniferous forests probably becoming established at higher elevations. However, later Eocene and Oligocene floras provide less evidence of the kinds of vegetational boundaries implied by the contrasts between the four floras discussed above. This may reflect in part a less adequate sample of coeval floras.

One time interval in the remainder of the Eocene and Oligocene contains enough fossil floras to permit an attempt at analyzing vegetational variability in the Rocky Mountain region.

Ten floras in Appendix I are from rocks of probable Chadronian age: Missoula, from westcentral Montana (245–246; Jennings, 1920); Christensen Ranch, Horse Prairie, and Medicine Lodge from southwestern Montana (151–152, 153–157, 159–160; the Beaverhead Basins floras of Becker, 1969); uppermost Bull Run from northeastern Nevada (202; Axelrod, 1966a, 1966b); Florissant from central Colorado (224–229; MacGinitie, 1953); Red Rock Ranch, Hermosa, and Hillsboro from the Rio Grande Rift of New Mexico (232, 233, 234; Axelrod & Bailey, 1976; Meyer, 1986); and a small flora from the White River Group in the Flagstaff Rim area of central Wyoming (240).

The Missoula flora was derived from a sequence of coal and lacustrine ash beds that Jennings (1920) believed were correlative with the lower part of the White River Formation in South Dakota. The flora has not been studied since 1920, and many of Jennings's identifications are questionable. However the flora appears to be dominated by *Metasequoia, Sequoia,* and one or more species of Betulaceae. *Equisetum, ?Thuites, ?Populus* sect. *Abaso, Acer,* and *?Cercidiphyllum* are also present. It is difficult to reach any conclusion about vegetation based on such a small assemblage of relatively ubiquitous taxa.

Becker (1969) considered the Beaverhead Basins floras to be of latest Oligocene to Miocene age, but this was based on the thickness of the local stratigraphic sequence and on floral correlation; the latter was in turn based on an incomplete understanding of the taxa involved. More recent geological and paleontological work suggests that the sections are thinner than originally thought, and that the "Medicine Lodge Beds," from which the floras were collected, may correlate with sediments producing Chadronian vertebrates (Fields et al., 1985). All three of the Beaverhead Basins floras represent mixed coniferous and deciduous broad-leaved forest, which Becker (1969) felt reflected a subhumid climate. The subhumid elements include such taxa as *Mahonia, Juniperus,* and various nanophyllous Leguminosae. Common broad-leaved deciduous taxa are *Fagopsis longifolia, Cercidiphyllum, Populus, Sassafras,* and various Betulaceae and Ulmoideae. Upsection changes in floral composition are relatively modest, although the upper two floras have 14 (Medicine Lodge) and 16 (Horse Prairie) species of conifers to the 10 species found in the lowest flora. There is a pronounced physiognomic change between the Christensen

Ranch flora and the upper two in that the percentage of species with entire-margined leaves increases from 18% to 34% and 37%. The significance of this shift is cast into some doubt by concomitant changes in depositional environment and floral diversity, and by the lower reliability of leaf margin data from coniferous vegetation (Wolfe, 1979), but taken at face value the increase in percentage of species with entire-margined leaves would indicate an increase in mean annual temperature from 7° to 12°C.

Axelrod (1966a, 1966b) stated that the upper Bull Run floras represented montane forest almost totally dominated by conifers, including *Abies, Picea, Pinus, Pseudotsuga, Tsuga, Chamaecyparis,* and *Thuja.* The angiosperm components are small-leaved and, with the exception of *Mahonia,* deciduous genera such as *Alnus, Betula, Ribes,* and *Zelkova.* This low diversity, strongly conifer-dominated assemblage contrasts markedly with the Beaverhead Basins floras, and although the upper Bull Run floras may be slightly older than those of the Beaverhead Basins (the highest locality is five feet below a tuff dated at 36 Ma; Axelrod, 1966a; Table 1), it seems probable that a difference in paleoelevation is also involved.

The small flora from the Chadronian of the Flagstaff Rim area was collected from clastic dike fillings that also preserve vertebrate skeletons (Emry, pers. comm., 1986). This peculiar mode of deposition makes comparisons between this flora and others questionable, but the low diversity (about six forms) and the small leaf size (microphylls or nanophylls) probably indicate relatively dry conditions. The identifiable taxa are *Mahonia, ?Ribes, ?*Ulmaceae, Leguminosae, and an undetermined conifer. This small flora may represent interfluve vegetation better than typical collections obtained from rocks deposited in paludal or lacustrine settings.

The Florissant flora is the most diverse from the Oligocene of the Rocky Mountain area. Based on a combination of floristic and physiognomic criteria, MacGinitie (1953) inferred that the Florissant fossil assemblage represented two main types of vegetation: a mesic, broad-leaved deciduous forest along streams and lakeshores and a drier scrub forest and grass vegetation on slopes and interfluve areas. The ten most common species in the flora comprise 60% of the specimens collected: *Fagopsis longifolia, Zelkova drymeja, Chamaecyparis, Typha, Populus crassa, Rhus stellariaefolia, Sequoia affinis, Cercocarpus*

myricaefolius, Staphylea acuminata, and *Athyana haydenii.* The broad-leaved evergreen component of the Florissant is not dominant, but the diversity and abundance of conifers is much less than in either the Beaverhead Basins or the upper Bull Run floras.

Chadronian floras from New Mexico (Axelrod & Bailey, 1976; Meyer, 1986) appear to represent two different types of vegetation. The Red Rock Ranch flora is numerically dominated by specimens of *Pinus* subsection *Balfourianae* and contains species of *Picea, Abies, Zelkova,* and possibly *Salix* and *Rosa* (Meyer, 1986). Based on a list by Farkas (1969), Axelrod & Bailey (1976) reported several additional taxa including *Fagopsis, Halesia, Mahonia, Rhus,* and *Sapindus,* but, with the exception of *Mahonia,* these were not confirmed by Meyer (1986). Although the Red Rock Ranch flora is small, on the basis of relatively high conifer diversity and abundance and low broad-leaf diversity, Meyer (1986) concluded that it most likely represents a mixed coniferous forest. This flora was correlated with Florissant (35 Ma) by Axelrod & Bailey (1976), but the more recent and direct radiometric date obtained by Meyer (1986) indicates the flora is no younger than 36.7 ± 1.1 Ma, or about 2 Ma older than Florissant.

The Hermosa and Hillsboro floras are derived from sediments associated with the infilling of the moat of the Emory caldera, and both were dated at about 32 Ma by Axelrod & Bailey (1976). New radiometric dates reported by Meyer (1986) indicate the Hillsboro flora is probably 28.1–30.6 Ma (Whitneyan or early Arikareean) and that the Hermosa flora is about 33.6 ± 1.0 Ma (Chadronian). The floras are similar in composition, with an overwhelming dominance of specimens of *Pinus* subsection *Balfourianae,* along with a few small leaves of *Mahonia,* and possibly *Picea* and *Crataegus.* These floristic and physiognomic attributes indicate a taiga-type forest growing under a cold temperate climate (Meyer, 1986). Axelrod & Bailey (1976) argued that the difference between the Red Rock Ranch and Hermosa/ Hillsboro floras was a response to higher paleoelevation of the latter floras; however, Meyer (1986) pointed out that these floras may bracket the major decrease in mean annual temperature and increase in mean annual range of temperature that occurred at about 33 Ma (Wolfe & Hopkins, 1967; Wolfe, 1986).

The pattern of geographic variation in Chadronian vegetation is less obvious than that of the earliest Bridgerian, and this can be attributed to several causes. First, the Chadronian floras are less tightly correlated and probably occurred over a longer interval of time, perhaps 5 Ma. Second, several of the floras are of low diversity or are not completely described, with the result that they are poorer samples of regional vegetation. Third, there may be a greater altitudinal range represented by the floras. Fourth, the youngest floras in the set (Hermosa/Hillsboro) may lie on the opposite side of a major temperature decrease from the other floras. In spite of these problems, the three floras of presumed intermediate elevation (Beaverhead Basins, Florissant, Red Rock Ranch) seem to have broadly similar compositions and to represent mixed coniferous and broad-leaved deciduous forest growing under a seasonally dry climate. The higher diversity of conifers and mesic taxa in the Montana floras may indicate higher rainfall and/ or lower rates of evapotranspiration in the northern part of the Rocky Mountains. The subhumid aspect of all of these floras when compared with those of similar age from the Pacific Northwest demonstrates the continuation of the pattern of regional climatic variation that began during the early Eocene/latest Paleocene.

The mid Tertiary climatic deterioration. Much of the evidence for the major decrease in mean annual temperature and increase in mean annual range of temperature that occurred at approximately 33 Ma is derived from lowland floras from the Pacific Coast of North America (Wolfe & Hopkins, 1967; Wolfe, 1971, 1986). Is there unambiguous evidence of this major climatological change in floras from the Rocky Mountain region? Presently this does not seem to be the case. Using the dates and correlations presented in Figure 3, there are six floras that closely follow after the 34 Ma date: Mormon Creek, Metzel Ranch, York Ranch, Ruby paper shales, Hermosa, and possibly Hillsboro. The dating of the Montana floras has been uncertain since their initial descriptions (Becker, 1960, 1961, 1972, 1973), and opinions on the age of the Mormon Creek flora have embraced some 20 Ma. Recent geological and mammalian biostratigraphic correlations suggest the Mormon Creek, Metzel Ranch, and York Ranch floras are of Orellan age (32.2–30.8 Ma) and that the Ruby paper shale flora is Whitneyan (30.8–29.2 Ma). These floras were judged by Becker (1960, 1961, 1972, 1973) to represent mixed coniferous and

broad-leaved deciduous forest and shrubland growing under temperate to dry-temperate climates. Although the Ruby paper shale flora is inferred to have been somewhat dryer than the other three, they all bear substantial resemblance to one another and to the older (Chadronian) Beaverhead Basins floras. As noted above, the New Mexican floras are derived from a setting of some paleotopographic and structural complexity, so that it is difficult to separate potential effects of elevation and regional climatic change.

Thus the only floras of suitable age do not provide good evidence of a major temperature decrease at 33 Ma. This absence of evidence may result from the confounding effects of changing elevations and dryer climates in the Rocky Mountains, or it may simply be a problem of insufficient data and poor stratigraphic control.

PRESENT METHODS AND FUTURE STUDY

Perhaps the most useful result of summarizing current knowledge and opinions in a field of study is that this activity reveals gaps in the data base and reveals possible directions for future research. At present, research in Tertiary paleobotany follows two main themes: the systematic/evolutionary approach is concerned primarily with describing new fossil forms and understanding their implications for the evolutionary history of lineages and relationships among living groups of plants; the paleoecological/environmental approach focuses largely on understanding habits of extinct species, structure of extinct vegetation, and patterns of ancient climates. Historically these approaches often were combined in the treatment of a single fossil flora. More recently, as standards have become higher and techniques more sophisticated in both approaches, workers have specialized on one or the other. This probably reflects a more general separation of ecology from systematics, but the disjunction in viewpoints should not be accepted as inevitable or desirable. Ecological and systematic approaches must be combined in order to reach a full understanding of evolution, because ecological data provide the context for understanding the genealogical changes that are inferred from systematic studies. Furthermore, in paleobotany both approaches are united at a practical level by the study of the same sites and specimens.

FIELD DATA

As noted in the section on the data base for Eocene and Oligocene floras, the stratigraphic and geographic distribution of sites is very uneven. The total number of sites from which collections have been made is also small, considering the commonness of plant fossils and the large outcrop area. The meagerness of the data set results from there being few paleobotanists, from a tendency for the same sites to be collected repeatedly, and from relatively small efforts toward finding new sites. The largest "holes" in the record would be filled by: 1) more late Eocene and Oligocene floras from the eastern Rocky Mountain area; 2) more Paleogene floras from the southern Rocky Mountains; and 3) more fluvially deposited late Eocene or Oligocene assemblages (or conversely, more Paleocene and early Eocene lacustrine assemblages).

Field data that would enhance reports of fossil plants include: number of quarry sites collected; size of quarry; precise locality information; stratigraphic unit; detailed lithological description; abundance of fossils and relative abundance of species; and, where available, biostratigraphic correlation, radiometric age, and paleomagnetic correlation. If such data were available, even as preliminary approximations, the published record of Tertiary fossils would be more useful for interpreting paleovegetation, paleoclimate, and possible associations of dispersed organs.

SYSTEMATICS

During the last 15 to 20 years several new methods have brought increased resolution and rigor to systematic studies of Tertiary angiosperms. Comparative studies of the leaf architecture of living dicotyledons have created a much firmer basis for interpreting the systematic affinities of fossil leaves (Hickey & Wolfe, 1975). The range of characters being studied has increased greatly, and important systematic data are now being gained from fossil cuticle (e.g., Upchurch, 1984a, 1984b; Jones, 1986), structure and ultrastructure of fossil pollen (e.g., Crepet et al., 1980), and from more detailed analyses of fossil flowers (e.g., Crepet & Daghlian, 1981, 1983). At the same time, more studies have come to base their systematic conclusions on multiple fossil organs belonging to the same species (e.g., Manchester & Crane, 1983; Wing & Hickey, 1984; Manchester, 1986). Finally, in many areas of paleobotany, refinements in methods of systematic analysis have resulted in sharper definition of characters and character states and have made the reasoning behind systematic decisions more explicit (e.g., Stein et al., 1984).

Although major advances have been made in

methodology, the vast majority of fossil angiosperms from western North America are as yet very poorly understood. For most times and places the floras either have not been described or the only descriptions are those of late-19th century workers whose goals were more biostratigraphic than systematic. New methods will have to be applied repeatedly before the botanical relationships of any significant number of Tertiary fossils will be understood.

Methodology has remained underdeveloped in the quantification of variability. Comparative leaf architecture was an important advance in analyzing higher-level systematic affinities but has been much less useful at the level of species. With few exceptions (e.g., Dolph, 1975; Burnham, 1986a, 1986b; Wing & Eckenwalder, 1987), paleobotanists have been little concerned with quantifying the variability of their taxa. Yet individuating taxa in a paleobotanical sample is the initial step in subsequent systematic, biostratigraphic, and paleoecological syntheses. Detection and quantification of low-level morphological variability is also a key to uncovering patterns of temporal change in closely spaced stratigraphic samples.

PALEOECOLOGY

Traditional paleoecological interpretation of fossil angiosperm floras has been based on floristic analogy and on leaf physiognomic analysis. The floristic method assumes that the ecological/climatic requirements of the fossil taxa were similar to those of their closest living relatives. This kind of direct analogy suffers from several defects (see Wolfe, 1979). First, it assumes that the botanical relationships of the fossils have been determined correctly. Second, it assumes that little evolutionary change has occurred in the climatic or ecological preferences of the lineages under study. Justification for both of these assumptions diminishes as one considers older floras, because evolution is more likely to have occurred in the intervening time, making it more difficult to determine close living relatives of older fossil plants. A third problem with floristic inference is that it implies that the present-day distribution of a taxon accurately reflects even its present climatic tolerances. Given the rapid climatic fluctuations typical of the last two million years, it may be that the current distributions of many taxa are strongly influenced by migration rate, plant competitors, or other nonclimatic factors (Davis, 1976).

The second commonly used method of paleovegetational/paleoclimatic inference is analysis of leaf physiognomy. Physiognomic analysis primarily relies on a relationship observed in living floras; the percent of species in a local flora that have entire-margined leaves rises with the mean annual temperature of the site (Bailey & Sinnott, 1915, 1916). Thus tropical floras have nearly 100% species with entire leaves, whereas temperate floras are dominated by species with toothed or lobed leaves. This relationship has been worked out with some precision based on the humid floras of East Asia (Wolfe, 1979). Studies based on smaller regions have been used to question the resolution of leaf-margin inferences (Dolph, 1976, 1978a, 1978b, 1979; Dolph & Dilcher, 1979), but the basic pattern of climate change as inferred from Tertiary floras agrees with data from a variety of other sources (e.g., Savin, 1977; Wolfe & Poore, 1982; Hutchison, 1982; Owen & Rea, 1985; Rea et al., 1985). Physiognomic analysis also considers the average size of leaves in a fossil assemblage, their apparent thickness, cuticle thickness, pubescence, the number of leaf types with drip tips, and the number of species that are probable lianes (those with cordate-based leaves). Generally these attributes increase with increasing tropicality of vegetation.

Although physiognomic analysis offers significant improvement on the floristic method, it has defects. In addition to their correlation with mean annual temperature, physiognomic characteristics of leaves are also correlated with water availability, intensity and angle of incident radiation, and a variety of other factors. Consequently, changes in the leaf physiognomy of fossil assemblages cannot always be read unambiguously as changes in mean annual temperature. An increase in climatically or edaphically induced water stress could produce vegetation with small, thick, entire-margined leaves and few lianes. Greater representation of canopy species in a fossil flora would produce an assemblage with smaller leaves (Roth & Dilcher, 1978). This is because canopy leaves tend to be smaller than interior leaves in order to radiate heat more efficiently and maintain an optimal photosynthetic rate. Perhaps the most serious factor biasing leaf physiognomic analysis of fossil assemblages is the probable overrepresentation of early successional and streamside plants, which grow close to sites of deposition in fluvial and volcanic settings (MacGinitie, 1969). Successional and riparian vegetation in most climatic zones is dominated by species with lobed, toothed, or compound

leaves, probably because these species hold individual leaves for only a short time, and these leaf shapes provide a large photosynthetic surface at a small cost of support tissue (Givnish, 1978). Thus a change in the frequency with which fossil vegetation was disturbed might produce a change in leaf physiognomy that might be interpreted as a change in mean annual temperature.

In spite of their defects, both the floristic and leaf physiognomic methods produce inferences about paleovegetation that are generally consistent with paleoclimatic reconstructions based on other, independent data sets. Furthermore, they generally agree with one another (e.g., MacGinitie, 1974; Hickey, 1977). The problem with these methods is not that they produce grossly incorrect interpretations of past vegetational structure, but rather that the inferences lack detail, frustrating the most interesting comparisons that might be made between extinct and living forests.

For instance, because of strong seasonality of light and a low angle of incident radiation, it is likely that the structure of high latitude, broad-leaved, evergreen forests in the early Tertiary was significantly different from that of living broad-leaved evergreen forests, even though the two types of vegetation are similar in leaf physiognomy and floristic composition. This hypothesis can only be examined by finding more ways to compare fossil and living vegetation. These new methods of comparison will probably require collecting data on the distribution of fossils in the sediment. These distributional data (e.g., alpha and beta diversity, relative abundance, spatial heterogeneity) may reflect actual synecological characteristics of the vegetation that produced a fossil assemblage; the difficulty in interpretation arises from the probability that taphonomic processes have also influenced the distribution of fossils. In spite of recent work on the taphonomy of fossil plants (Spicer, 1981; Scheihing & Pfefferkorn, 1984; Spicer & Greer, 1986; Ferguson, 1985; Gastaldo, 1986; Burnham & Spicer, 1986; Spicer & Wolfe, 1987), there are as yet no general recommendations for how leaf assemblages can be sampled to reflect best given characteristics of the former vegetation. This kind of work will have to be done in order to make the best use of the paleoecological information preserved in fossil plant assemblages.

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APPENDIX I

Name, source, North American land mammal age, and stratigraphic position of localities in Figures 3 and 4. Abbreviations for North American Land Mammal Ages (NALMA):

GB = Graybullian	WA = Wasatchian	UI = Uintan	OR = Orellan
LY = Lysitean	GA = Gardnerbuttean	DU = Duschesnean	WH = Whitneyan
LC = Lostcabinian	BR = Bridgerian	CH = Chadronian	AR = Arikareean

Number	Locality	Source	NALMA	Stratigraphic Unit
1	USNM 14048	Hickey, 1977	LC	upper Camels Butte Member, Golden Valley Fm.
2	USNM 14141	Hickey, 1977	LC	upper Camels Butte Member, Golden Valley Fm.
3	USNM 14117	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
4	USNM 14094	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
5	USNM 14092	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
6	USNM 14089	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
7	USNM 14088	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
8	USNM 14054	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
9	USNM 14099	Hickey, 1977	LC	upper Camels Butte Member, Golden Valley Fm.
10	USNM 14066	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
11	USNM 14052	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
12	USNM 14053	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
13	USNM 14056	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
14	USNM 14068	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
15	USNM 14025	Hickey, 1977	GB	lower Camels Butte Member, Golden Valley Fm.
16	USGS 8892	unpublished	WA	Wasatch Fm., above Roland Coal
17	USGS 8891	unpublished	WA	Wasatch Fm.
18	USGS 8890	unpublished	WA	Wasatch Fm.
19	USGS 9394	unpublished	LC	upper Wasatch Fm. on Pumpkin Buttes
20	USGS 9483	unpublished	WA	?
21	USGS 6985	unpublished	?WA	Hanna Fm.?
22	USGS 6978	unpublished	?WA	Hanna Fm.?
23	Little Mountain; PA116	MacGinitie, 1969	GA/BR	upper Wilkins Peak Mbr., Green River Fm.
24	USGS 8588	unpublished	?LC	Wasatch Fm.
25	USGS 5263	unpublished	?LC	Wasatch Fm.
26	USGS 5255	unpublished	?LC	Wasatch Fm.
27	USGS 9495	unpublished	?LC	Niland Tongue, Wasatch Fm.
28	USGS 9179	unpublished	?LC	Niland Tongue, Wasatch Fm.
29	USGS 9397	unpublished	LC	Niland Tongue, Wasatch Fm.
30	USGS 4811	unpublished	?LC	Niland Tongue, Wasatch Fm.
31	Eden Valley	Kruse, 1954; MacGinitie, 1969	BR	base of Laney Mbr., Green River Fm.
32	USGS 9051; Schoening	MacGinitie, 1974	LC	lower Lost Cabin Mbr., Wind River Fm.
33	USGS 9537	unpublished	LC	Lost Cabin Mbr., Wind River Fm.
34	USGS 9040; Rate Homestead	MacGinitie, 1969	UI	Wagonbed Fm.

APPENDIX I. Continued.

Number	Locality	Source	NALMA	Stratigraphic Unit
35	USGS 8784	unpublished	LC	Lost Cabin Mbr., Wind River Fm.
36	USGS 9052; Boysen Locality; PA-111	MacGinitie, 1974	GA	upper Lost Cabin Mbr., Wind River Fm.
37	USGS 8770; Crowheart Locality	unpublished	?LC	upper Wind River Fm.
38	Tipperary; USGS 8785	MacGinitie, 1974	BR	Aycross Fm.
39	Coyote Creek	MacGinitie, 1974	?BR	Aycross Fm.
40	Rhodes Ranch	MacGinitie, 1974	?BR	Aycross Fm.
41	Wind River flora; USGS 8912; PA-104	Leopold & MacGinitie, 1972	LC	lower Aycross Fm.
42	Kisinger Lakes	MacGinitie, 1974	BR	Aycross Fm.
43	USGS 9519; Princeton "Willwood"	unpublished	LC/GA	tuffaceous lake beds above Willwood Fm. (Bown, 1982)
44	USGS 10022; Princeton "Willwood"	unpublished	LC/GA	tuffaceous lake beds above Willwood Fm. (Bown, 1982)
45	USGS 8496; Princeton "Willwood"	unpublished	LC/GA	tuffaceous lake beds above Willwood Fm. (Bown, 1982)
46	USGS 8586	unpublished	?BR	Aycross Fm.
47	USGS 8909	unpublished	?BR	Aycross Fm.
48	USGS 6389	unpublished	?	?
49	USGS 6177	unpublished	?	?
50	USGS 8894; Jim Creek	unpublished	LC	uppermost Willwood Fm.
51	T2; USNM 37687	Wing, 1981	LC	lower Tatman Fm.
52	TAT79; USNM 37686	Wing, 1981	LC	lower Tatman Fm.
53	BCT4; USNM 37685	Wing, 1981	LC	lower Tatman Fm.
54	BCT3; USNM 37684	Wing, 1981	LC	lower Tatman Fm.
55	BCT2; USNM 37683	Wing, 1981	LC	lower Tatman Fm.
56	BCT; USNM 37682	Wing, 1981	LC	lower Tatman Fm.
57	WhBgL; USNM 37681	Wing, 1981	LC	lower Tatman Fm.
58	WhBg; USNM 37680	Wing, 1981	LC	lower Tatman Fm.
59	B; USNM 37679	Wing, 1981	LC	lower Tatman Fm.
60	MQ; USNM 37678	Wing, 1981	LC	upper Willwood Fm.
61	AL; USNM 37677	Wing, 1981	LC	upper Willwood Fm.
62	Brosh; USNM 37676	Wing, 1981	LC	upper Willwood Fm.
63	T; USNM 37675	Wing, 1981	LC	upper Willwood Fm.
64	Fl; USNM 37674	Wing, 1981	LC	upper Willwood Fm.
65	TL; USNM 37673	Wing, 1981	LC	upper Willwood Fm.
66	CQ; USNM 37672	Wing, 1981	LC	upper Willwood Fm.
67	15M; USNM 37671	Wing, 1981	LC	upper Willwood Fm.
68	15ME; USNM 37670	Wing, 1981	LC	upper Willwood Fm.
69	SL; USNM 37669	Wing, 1981	LC	upper Willwood Fm.
70	M; USNM 37668	Wing, 1981	LC	upper Willwood Fm.
71	A; USNM 37667	Wing, 1981	LC	upper Willwood Fm.
72	MBR; USNM 37666	Wing, 1981	LY	middle Willwood Fm.
73	Pn; USNM 37560	Wing, 1981	LY	middle Willwood Fm.
74	125; USNM 37664	Wing, 1981	LY	middle Willwood Fm.

APPENDIX I. Continued.

Number	Locality	Source	NALMA	Stratigraphic Unit
75	67; USNM 37663	Wing, 1981	LY	middle Willwood Fm.
76	320; USNM 37662	Wing, 1981	LY	middle Willwood Fm.
77	H; USNM 37661	Wing, 1981	GB	middle Willwood Fm.
78	281-3; USNM 37660	Wing, 1981	GB	middle Willwood Fm.
79	281-2; USNM 37659	Wing, 1981	GB	middle Willwood Fm.
80	281; USNM 37657	Wing, 1981	GB	middle Willwood Fm.
81	DCF; USNM 37656	Wing, 1981	GB	middle Willwood Fm.
82	DCl; USNM 37655	Wing, 1981	GB	middle Willwood Fm.
83	LB; USNM 37654	Wing, 1981	GB	middle Willwood Fm.
84	RR5; USNM 37653	Wing, 1981	GB	lower Willwood Fm.
85	98; USNM 37652	Wing, 1981	GB	lower Willwood Fm.
86	RR1; USNM 37626	Wing, 1981	GB	lower Willwood Fm.
87	WCS8-2; USNM 37651	Wing, 1981	GB	lower Willwood Fm.
88	WCS8-1; USNM 37650	Wing, 1981	GB	lower Willwood Fm.
89	RC; USNM 37649	Wing, 1981	GB	lower Willwood Fm.
90	HsII; USNM 37648	Wing, 1981	GB	lower Willwood Fm.
91	Hs; USNM 37563	Wing, 1981	GB	lower Willwood Fm.
92	UU; USNM 37646	Wing, 1981	GB	lower Willwood Fm.
93	BRII; USNM 37645	Wing, 1981	GB	lower Willwood Fm.
94	BR1.5; USNM 37644	Wing, 1981	GB	lower Willwood Fm.
95	BR; USNM 37643	Wing, 1981	GB	lower Willwood Fm.
96	Bs; USNM 37642	Wing, 1981	GB	lower Willwood Fm.
97	CnII; USNM 37641	Wing, 1981	GB	lower Willwood Fm.
98	CnI; USNM 37640	Wing, 1981	GB	lower Willwood Fm.
99	P; USNM 37639	Wing, 1981	GB	lower Willwood Fm.
100	S; USNM 37638	Wing, 1981	GB	lower Willwood Fm.
101	WCS6; USNM 37637	Wing, 1981	GB	lower Willwood Fm.
102	GER; USNM 37591	Wing, 1981	GB	lower Willwood Fm.
103	RR4; USNM 37635	Wing, 1981	GB	lower Willwood Fm.
104	USGS 6177	Wing, 1981	GB	lower Willwood Fm.
105	LHE; USNM 37633	Wing, 1981	GB	lower Willwood Fm.
106	VSI; USNM 37584	Wing, 1981	GB	lower Willwood Fm.
107	RR2; USNM 37631	Wing, 1981	GB	lower Willwood Fm.
108	LW; USNM 37630	Wing, 1981	GB	lower Willwood Fm.
109	LR1; USNM 37629	Wing, 1981	GB	lower Willwood Fm.
110	HFU; USNM 37628	Wing, 1981	GB	upper Fort Union Fm.
111	FUCS1; USNM 37627	Wing, 1981	GB	upper Fort Union Fm.
112	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Lamar River Fm. on Specimen Ridge
113	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Sepulcher Fm. on Yellowstone River
114	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Sepulcher Fm. on Crescent Hill

APPENDIX I. Continued.

Number	Locality	Source	NALMA	Stratigraphic Unit
115	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Sepulcher Fm. near Elk Creek
116	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Sepulcher Fm. on N. bank of Lamar River
117	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Sepulcher Fm. opposite mouth Hellroaring Crk.
118	Yellowstone flora (Princeton)	Dorf, unpubl.	WA/BR	Sepulcher Fm., east side, Yellowstone river
119	Bearpaw Mtns.; USGS 8902	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
120	Bearpaw Mtns.; USGS 9959	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
121	Bearpaw Mtns.; USGS 9186	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
122	Bearpaw Mtns.; USGS 9957	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
123	Bearpaw Mtns.; USGS 9355	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
124	Bearpaw Mtns.; USGS 9222	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
125	Bearpaw Mtns.; USGS 9354	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
126	Bearpaw Mtns.; USGS 9958	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
127	Bearpaw Mtns.; USGS 9960	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
128	Bearpaw Mtns.; USGS 9187	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
129	Bearpaw Mtns.; USGS 9218	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
130	Bearpaw Mtns.; USGS 9956	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
131	Bearpaw Mtns.; USGS 9124	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
132	Bearpaw Mtns.; USGS 9216	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
133	Bearpaw Mtns.; USGS 9146	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
134	Bearpaw Mtns.; USGS 9137	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
135	Bearpaw Mtns.; USGS 9133	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wastach equivalent
136	Bearpaw Mtns.; USGS 9290	Brown & Pecora, 1949	BR	unnamed volcanics overlying Wasatch equivalent
137	Upper Ruby River 1 (blocky shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
138	Upper Ruby River 2 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
139	Upper Ruby River 3 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
140	Upper Ruby River 4 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
141	Upper Ruby River 5 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
142	Upper Ruby River 6 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
143	Upper Ruby River 7 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
144	Upper Ruby River 8 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
145	Upper Ruby River 9 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
146	Upper Ruby River 10 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
147	Upper Ruby River 11 (paper shale)	Becker, 1961	WH	Passamari Mbr., Renova Fm.
148	Mormon Creek	Becker, 1960	OR	Dunbar Crk. Mbr., Renova Fm.
149	Metzel Ranch	Becker, 1972	OR	Dunbar Crk. Mbr., Renova Fm.
150	York Ranch	Becker, 1973	OR	Dunbar Crk. Mbr., Renova Fm.
151	Christensen Ranch (lower)	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
152	Christensen Ranch (upper)	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
153	Horse Prairie	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)

APPENDIX I. Continued.

Number	Locality	Source	NALMA	Stratigraphic Unit
154	Horse Prairie	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
155	Horse Prairie	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
156	Horse Prairie	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
157	Horse Prairie	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
158	Medicine Lodge	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
159	Medicine Lodge	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
160	Medicine Lodge	Becker, 1969	CH?	"Medicine Lodge Beds" (Fields et al., 1985)
161	Targhee Flora	Axelrod, 1968	?	?
162	Coal Creek, Idaho	Axelrod, 1968	UI	Challis Volcanics
163	Democrat Creek	Axelrod, 1968	UI	Challis Volcanics
164	Bullion Gulch	Axelrod, 1968	UI	Challis Volcanics
165	Germer Basin	Edelman, 1975	UI	Germer Tuffaceous Mbr., Challis Volcanics
166	Salmon flora	Brown, 1937; Axelrod, 1968	UI/DU	Germer Tuffaceous Mbr., Challis Volcanics
167	Thunder Mountain	Axelrod, 1966b, 1968	UI	"Dewey Beds," Challis Volcanics
168	Republic flora, main locality	Wolfe & Wehr, 1987	UI	Klondike Mtn. Fm.
169	Republic flora, Resner Canyon	Wolfe & Wehr, 1987	UI	Klondike Mtn. Fm.
170	Republic flora, Graphite Creek	Wolfe & Wehr, 1987	UI	Klondike Mtn. Fm.
171	Roslyn	Wolfe, 1968; Axelrod, 1968	?	?
172	Clarno Nut Beds; OMSI-225	Scott, 1954; Bones, 1979	BR	Clarno Fm.
173	W. Branch Creek; USGS 8637; OMSI-230	Manchester, 1986	WA-BR	Clarno Fm.
174	Hancock Canyon mudflow; OMSI-49	Manchester, 1986	BR-DU	Clarno Fm.
175	Hancock Tree Canyon; OMSI-69	Manchester, 1986	UI-DU	Clarno Fm.
176	Gosner Road; OMSI-238	Manchester, 1986	BR-UI	Clarno Fm.
177	Indian Rocks; OMSI-239	Manchester, 1986	BR-UI	Clarno Fm.
178	W. Branch Crk. lacustrine; OMSI-226	Manchester, 1986	BR-UI	Clarno Fm.
179	W. Branch Crk. shale; OMSI-228	Manchester, 1986	BR-UI	Clarno Fm.
180	Alex Canyon lacustrine, OMSI-229	Manchester, 1986	BR-UI	Clarno Fm.
181	Dry Hollow mudflow tuff; OMSI-253	Manchester, 1986	UI-DU	Clarno Fm.
182	Lower Cedarville flora	Axelrod, 1966a	DU	lower Cedarville Fm.
183	Susanville flora	Wolfe, pers. comm.		
184	Iowa & Independence Hill; loc. 42	MacGinitie, 1941	WA	Ione Fm.
185	Chalk Bluffs; P3318	MacGinitie, 1941	WA	Ione Fm.
186	Chalk Bluffs; P3324	MacGinitie, 1941	WA	Ione Fm.
187	Chalk Bluffs; P3325	MacGinitie, 1941	WA	Ione Fm.
188	Chalk Bluffs; P3345	MacGinitie, 1941	WA	Ione Fm.
189	Buckeye Flat; loc. 104	MacGinitie, 1941	WA	Ione Fm.
190	Buckeye Flat; P3370	MacGinitie, 1941	WA	Ione Fm.
191	Quaker Flat; P3346	MacGinitie, 1941	WA	Ione Fm.
192	Sailor Flat; P3347	MacGinitie, 1941	WA	Ione Fm.
193	Cherokee Mine; loc. 206	MacGinitie, 1941	WA	Ione Fm.

Appendix I. Continued.

Number	Locality	Source	NALMA	Stratigraphic Unit
194	Corral Hollow	Axelrod, 1968		
195	Coal Creek, Nevada	Axelrod, 1968		
196	Coal Mine Canyon palynoflora	Axelrod, 1966a, 1968	WA/GA	Elko Fm.
197	Bull Run flora (lower; Mori Road)	Axelrod, 1966a, 1968	DU	"Mori Rd. Fm."
198	Bull Run flora (lower; Summit)	Axelrod, 1966a, 1968	DU/CH	"I L Fm."
199	Bull Run flora (lower)	Axelrod, 1966a, 1968	DU/CH	"I L Fm."
200	Bull Run flora (upper)	Axelrod, 1966a, 1968	DU/CH	"Chicken Creek Fm."
201	Bull Run flora (upper)	Axelrod, 1966a, 1968	DU/CH	"Chicken Creek Fm."
202	Bull Run flora (upper)	Axelrod, 1966a, 1968	CH	"Chicken Creek Fm."
203	Copper Basin flora	Axelrod, 1966a, 1968	DU	Deadhorse Tuff
204	Sage Creek	Axelrod, 1968		
205	Rainbow, Utah; PA-107	MacGinitie, 1969	UI	upper Parachute Creek Mbr., Green River Fm.
206	Wardell Ranch; PA-106	MacGinitie, 1969	UI	upper Parachute Creek Mbr., Green River Fm.
207	West of Wardell Ranch; PA-321	MacGinitie, 1969	UI	upper Parachute Creek Mbr., Green River Fm.
208	Stewart Gulch; PA-326	MacGinitie, 1969	UI	430 feet above Mahogany Ledge, Green River Fm.
209	North Park; USGS 5987	unpublished	WA	Coalmont Fm.
210	North Park; USGS 6102	unpublished	WA	Coalmont Fm.
211	North Park; USGS 6437	unpublished	WA	Coalmont Fm.
212	North Park; USGS 5994	unpublished	WA	Coalmont Fm.
213	North Park; USGS 6110	unpublished	WA	Coalmont Fm.
214	North Park; USGS 6105	unpublished	WA	Coalmont Fm.
215	North Park; USGS 6103	unpublished	WA	Coalmont Fm.
216	North Park; USGS 5991	unpublished	WA	Coalmont Fm.
217	North Park; USGS 6107	unpublished	WA	Coalmont Fm.
218	North Park; USGS 6000	unpublished	WA	Coalmont Fm.
219	North Park; USGS 6111	unpublished	WA	Coalmont Fm.
220	North Park; USGS 6005	unpublished	WA	Coalmont Fm.
221	North Park; USGS 5997	unpublished	WA	Coalmont Fm.
222	North Park; USGS 6440	unpublished	WA	Coalmont Fm.
223	North Park; USGS 9446	unpublished	WA	Coalmont Fm.
224	Florissant; Denver Museum locality	MacGinitie, 1953	CH	Florissant Fm.
225	Florissant; P3731	MacGinitie, 1953	CH	Florissant Fm.
226	Florissant; P3732	MacGinitie, 1953	CH	Florissant Fm.
227	Florissant; P3733	MacGinitie, 1953	CH	Florissant Fm.
228	Florissant; Princeton locality	MacGinitie, 1953	CH	Florissant Fm.
229	Florissant; Scudder's locality	MacGinitie, 1953	CH	Florissant Fm.
230	unnamed	Tidwell et al., 1981	LY	Rosarita Mbr., San Jose Fm.
231	Galisteo palynoflora	Leopold & MacGinitie, 1972	UI	Galisteo Fm.
232	Red Rock Ranch	Meyer, 1986	CH	Red Rock Ranch Fm.
233	Hermosa	Meyer, 1986	CH	Mimbres Peak Fm.?
234	Hillsboro	Meyer, 1986	WH/AR	sediments overlying Emory caldera lake beds

APPENDIX I. Continued.

Number	Locality	Source	NALMA	Stratigraphic Unit
235	Barilla	Berry, 1919	DU?	Huelster Fm.
236	unnamed	Wilson, pers. comm.		
237	unnamed	Wilson, pers. comm.		
238	unnamed	Wilson, pers. comm.		
239	unnamed	Wilson, pers. comm.		
240	unnamed	Emry, pers. comm.	CH	White River Fm., below ash D
241	Poison Springs palynoflora	Leopold & MacGinitie, 1972	CH	White River Fm.
242	Creede, 5-Mile Bridge; 571A, B, C	Axelrod, 1987	AR	Creede Fm.
243	Creede, Birdsey Gulch; 574A, B, C	Axelrod, 1987	AR	Creede Fm.
244	Creede, Dry Gulch; 572A, B, C, D	Axelrod, 1987	AR	Creede Fm.
245	Creede, Wason Cliffs; 573A, B, C, D	Axelrod, 1987	AR	Creede Fm.
246	Missoula (loc. 165)	Jennings, 1920	CH	Renova Fm.?
247	Missoula (loc. 196)	Jennings, 1920	CH	Renova Fm.?
248	LaPorte			
249	Bridge Creek			
250	Alvord Creek			
251	Cow Creek			

APPENDIX II.

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